

Sap flow characteristics and physiological adjustments of two dominant tree species in pure and mixed plantations in the semi-arid Loess Plateau of China

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Abstract: It is essential to understand the water consumption characteristics and physiological adjustments of tree species under drought conditions, as well as the effects of pure and mixed plantations on these characteristics in semi-arid regions. In this study, the normalized sap flow (SF_n), leaf water potential, stomatal conductance (g_s), and photosynthetic rate (P_r) were monitored for two dominant species, i.e., *Pinus tabulaeformis* and *Hippophae rhamnoides*, in both pure and mixed plantations in a semi-arid region of Chinese Loess Plateau. A threshold-delay model showed that the lower rainfall thresholds (R^L) for *P. tabulaeformis* and *H. rhamnoides* in pure plantations were 9.6 and 11.0 mm, respectively, and the time lags (τ) after rainfall were 1.15 and 1.76 d for corresponding species, respectively. The results indicated that *P. tabulaeformis* was more sensitive to rainfall pulse than *H. rhamnoides*. In addition, strong stomatal control allowed *P. tabulaeformis* to experience low g_s and P_r in response to drought, while maintaining a high midday leaf water potential (Ψ_m). However, *H. rhamnoides* maintained high g_s and P_r at a low Ψ_m expense. Therefore, *P. tabulaeformis* and *H. rhamnoides* can be considered as isohydric and anisohydric species, respectively. In mixed plantation, the values of R^L for *P. tabulaeformis* and *H. rhamnoides* were 6.5 and 8.9 mm, respectively; and the values of τ were 0.86 and 1.61 d for corresponding species, respectively, which implied that mixed afforestation enhanced the rainfall pulse sensitivity for both two species, especially for *P. tabulaeformis*. In addition, mixed afforestation significantly reduced SF_n , g_s , and P_r for *P. tabulaeformis* ($P < 0.05$), while maintaining a high leaf water potential status. However, no significant effect of mixed afforestation of *H. rhamnoides* was observed at the expense of leaf water potential status in response to drought. Although inconsistent physiological responses were adopted by these species, the altered water consumption characteristics, especially for *P. tabulaeformis* indicated that the mixed afforestation requires further investigation.

Keywords: normalized sap flow; physiological adjustments; mixed afforestation; *Pinus tabulaeformis*; *Hippophae rhamnoides*

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Received 2017-11-12; revised 2018-01-30; accepted 2018-07-10

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1 Introduction

Vegetation restoration and reforestation of degraded land are useful forest management practices for the soil erosion conservation and hydrological regime regulation (Swaffer et al., 2014; Jian et al., 2015). By increasing biodiversity and the variety of ecological niches, mixed plantations may be more resistant to external disturbances, such as storms or disease attacks, compared with pure plantations (Zapater et al., 2013; Zhang et al., 2017). However, vegetation deterioration and ecological degradation have been observed in some mixed plantations because water supplies could not meet the demand for co-existing species, especially in arid and semi-arid regions (Chen et al., 2008; Yang et al., 2015). Some researchers have suggested that water shortage exerts a profound influence on water consumption, integrity of plant hydraulic systems, and carbon assimilation (Franks et al., 2007; Silvertown et al., 2015). Therefore, improved understanding of water consumption and drought tolerance strategies of species grown in pure and mixed plantations is needed to evaluate the most appropriate tree species, planting regimes, and forest management practices that will effectively respond to climate uncertainties in the further (Du et al., 2011).

Rainfall is essential to prevent plant mortality caused by drought (West et al., 2007). Analysis of the effect of rainfall pulses on plant water consumption is fundamental to acknowledge species sensitivity to rainfall pulses, as well as how these responses affect species adaptation to their habitats (Zhao and Liu, 2010). A threshold-delay model has been widely used to describe the effect of rainfall pulses on plant water consumption (Ogle and Reynolds, 2004). A threshold level of rainfall stimulates plant water use, and the time lags of tree and shrub responses have been investigated and evaluated by this model (Ivans et al., 2006; Zhao and Liu, 2010).

Plants undergo different physiological adjustments in the trade-off among water consumption, leaf water potential, and carbon gain to adapt to frequent drought stress (West et al., 2007; Silvertown et al., 2015). Several of these adjustments have been studied, including reliance on deep root systems (Yang et al., 2015), delayed stomatal closure (Tang et al., 2014), maintenance of high photosynthetic rate (Zhu et al., 2015), and adjustments in leaf water potential (McDowell et al., 2008). For example, the classification of isohydric and anisohydric species has been widely used to identify the balance between stomatal control, leaf water potential status, and carbon gain in response to drought conditions (Franks et al., 2007; Zapater et al., 2013). Isohydric species may experience smaller variations in leaf water potential through stomatal control regardless of carbon gain, whereas anisohydric species maintain stable carbon gain and stomatal conductance (g_s) at the expense of leaf water potential (West et al., 2007). However, Franks et al. (2007) found that some anisohydric species, such as *Eucalyptus gomphocephala*, exhibit strong stomatal regulation in response to limited soil water conditions and show isohydrodynamic characteristics. Zapater et al. (2013) attributed this altered physiological characteristics to a trade-off strategy between water consumption and carbon allocation, and they also related it to the root architecture system. Research into the water consumption and root systems, and further investigation into the role of physiological variables, such as leaf water potential, stomatal control, and carbon gain are needed to fully understand plant strategies for drought tolerance.

To overcome severe soil erosion and habitat degradation in Chinese Loess Plateau, government launched the "Grain-for-Green" project in the last decade, and plantations now occupy more than 59% of the region's total forest area (Jian et al., 2015). Due to their high drought tolerance and economic value, *Pinus tabulaeformis* and *Hippophae rhamnoides* are the main plantation species planted for ecological restoration in this region (Li et al., 2016). Mixed afforestation with these two species has also been widely used in the initial plantation stage, as mixed plantations generally show a higher plant survival rate and soil conservation capacity compared with pure plantations (Meng et al., 2008). In addition, evapotranspiration far exceeds annual precipitation in the Loess Plateau, and this imbalance may become acute for plant growth (Chen et al., 2015; Gao et al., 2018). Seasonal variations of water consumption under drought conditions for *P. tabulaeformis* or *H. rhamnoides* in pure plantations have been investigated in this region (Fang et al., 2016; Jian et al., 2016; Wen et al., 2017). However, physiological adjustments to drought and the effect of mixed afforestation on water consumption and physiological adjustments of these species have not been investigated.

The year 2015 was the driest year recorded in the Loess Plateau, with only 58.9% of the average precipitation since 1988. For species selection and plantation management practices in this region, variations in water consumption and physiological variables, including stem sap flow (SF), leaf water potential, g_s , and photosynthetic rate (P_r), were examined for 14-year-old planted *P. tabuliformis* and *H. rhamnoides* in pure and mixed plantations in 2015. The objectives were to (1) investigate the rainfall pulse sensitivities and physiological adjustments of the two species under drought conditions in pure plantations, and (2) identify whether water consumption characteristics and physiological adjustments for specific species were altered in mixed plantation.

2 Materials and methods

2.1 Study area and description of plantations

The study was conducted at the Ansai Station of the Chinese Academy of Sciences (36.51°N, 109.19°E; 1231 m a.s.l.) in the central part of the Chinese Loess Plateau. The climate is temperate semi-arid, with mean annual precipitation of 492.7 (± 129.4) mm and annual mean air temperature of 10.4°C (± 0.5)°C, according to the meteorological records during the period 1988–2015 in Ansai County. The loess in this region is characterized as silt loam with a depth of 50–190 m, depending on topography, with low organic carbon and nutrient contents (Xu et al., 2010).

Three adjacent plantations planted in 2002 were selected, i.e., a pure *P. tabuliformis* plantation, a pure *H. rhamnoides* plantation, and a *P. tabuliformis*-*H. rhamnoides* mixed plantation. A study plot of 20 m \times 20 m was established for each plantation type. The plantation density was typical of the central part of the Loess Plateau, i.e., stem densities were 1667 stems/hm² in pure *P. tabuliformis* plantation, and 10,000 stems/hm² in pure *H. rhamnoides* plantation, respectively. The stem densities in the corresponding mixed plantations were 1111 and 3333 stems/hm², respectively.

According to a plot survey conducted in July 2015, the stem densities of *P. tabuliformis* and *H. rhamnoides* in pure plantations were 1175 and 1900 stems/hm², respectively. The average height was 3.39 (± 0.47) m, average trunk diameter at breast height (1.3 m) was 59.5 (± 2.3) mm, and average canopy radius was 1.41 (± 0.28) m for *P. tabuliformis*. The average height was 3.3 (± 0.58) m, average trunk diameter at ground height (0.3 m) was 51.1 (± 1.7) mm, and average canopy radius was 0.95 (± 0.35) m for *H. rhamnoides*. From June to August 2015, the average leaf area index (LAI) was 1.78 (± 0.17) m²/m² in *P. tabuliformis* pure plantation and 1.81 (± 0.54) m²/m² in *H. rhamnoides* pure plantation, respectively, according to monthly monitored values using an LAI-2000 plant canopy analyzer (LI-Cor, Lincoln, Nebraska, USA). The dominant herbaceous species were *Glycyrrhiza uralensis* and *Bothriochloa ischaemum* in pure *P. tabuliformis* and *H. rhamnoides* plantations, respectively.

In mixed plantation, the stem densities of *P. tabuliformis* and *H. rhamnoides* were 850 and 1775 stems/hm², respectively. The average height was 3.68 (± 0.39) m, average trunk diameter was 62.7 (± 1.8) mm, and average canopy radius was 1.26 (± 0.29) m for *P. tabuliformis*. The average height was 3.13 (± 0.47) m, average trunk diameter was 53.6 (± 1.9) mm, and average canopy radius was 0.93 (± 0.36) m for *H. rhamnoides*. From June to August 2015, the average LAI was 2.06 (± 0.36) m²/m² in mixed plantation. The dominant herbaceous species were *B. ischaemum* and *Artemisia gmelinii* in mixed plantation.

2.2 Environmental variables

Meteorological variables have been measured less than 400 m from the selected plantation plots since 1999. Half hourly net radiation (R_n) (Model CNR-1, Kipp & Zonen Inc., Delft, The Netherlands), air relative humidity and temperature (HMP45C, Campbell Scientific Inc., Logan, UT, USA), rainfall amount (Model 52203, RM Young Inc., Traverse City, MI, USA), and soil heat flux (Model HFP01, Campbell Scientific Inc., UAS) were measured and stored using a CR1000 datalogger (Campbell Scientific Inc., USA). The soil water content (SWC) was continuously monitored at depths of 10, 20, 50, 100, and 150 cm in the three plantation plots using EM50 (Decagon Inc., Pullman, WA, USA).

Daily potential evapotranspiration (ET_p , mm) was calculated as follows (Priestley and Taylor, 1972):

$$ET_p = 1.26((R_n - G)s) / (s + \gamma), \quad (1)$$

where R_n and G are the net radiation (W/m^2) and soil heat flux (W/m^2), respectively; s is the slope of a function relating saturation vapor pressure to temperature (kPa/K); and γ is the psychrometric constant (kPa/K).

2.3 Sap flow measurements

Using Granier-type thermal dissipation probes (TDP) following Granier (1987), SF was monitored in a total of 25 individuals for these species during the growing season, from 5 June (DOY (day of the year) 156) to 26 September (DOY 269), 2015 (Table 1). To preserve the monitored trees, we established the equation between trunk diameter and sapwood width based on 20 unmonitored individual core samples for each species. Core samples were obtained using an increment borer, and the color difference between sapwood and heartwood was large.

In pure plantation, 7 individuals of *P. tabuliformis* were selected with a trunk diameter of 42–65 mm and a canopy radius of 1.01–1.56 m. Six individuals were selected for *H. rhamnoides* with a trunk diameter of 36–63 mm and a canopy radius of 0.84–1.17. In mixed plantation, it was important to select individuals of *H. rhamnoides* that were adjacent to selected individuals of *P. tabuliformis*, because one objective of this study was to identify the mixed plantation effect on water consumption and physiological adjustments for these two species. First, we selected 6 individuals of *P. tabuliformis* with a trunk diameter of 43–70 mm and a canopy radius of 1.18–1.48 m. Each *H. rhamnoides* was selected within 2 m of a trunk of *P. tabuliformis*, creating 6 pairs (Fig. S1). The 6 selected *H. rhamnoides* individuals had a trunk diameter of 38–67 mm and a canopy radius of 0.89–1.24 m. The 2-m radius was used to ensure potential interactions between *P. tabuliformis* and *H. rhamnoides* individuals. In our earlier work, it had been shown that the majority of lateral roots distance for *P. tabuliformis* and *H. rhamnoides* extended twice the distance of the corresponding canopy radius. The minimum canopy radius for selected *P. tabuliformis* individuals was 1.18 m; therefore, it was calculated that the minimum radius of the majority of lateral roots was approximately 2.36 m.

A pair of TDPs of the diameters of 10 and 2 mm was used for both *P. tabuliformis* and *H. rhamnoides*, respectively. The probes were uniformly and horizontally installed on the north side of the trunks at breast and ground heights for selected *P. tabuliformis* and *H. rhamnoides* individuals. The probes were packaged in aluminum foil to prevent thermal influences from ambient environmental variation. The SF data were measured at 30 s intervals and stored as half hour averages using a CR1000 data logger (Campbell Scientific Inc., USA) with an AM16/32A multiplexer (Campbell Scientific Inc., USA).

The standard sap flux density (F_d , $g/(m^2 \cdot s)$) can be calculated according to the equation suggested by Granier (1987):

$$F_d = 119((\Delta T_M - \Delta T) / \Delta T)^{1.231}, \quad (2)$$

where ΔT_M is the maximum temperature ($^{\circ}C$); and ΔT is the temperature difference between unheated and heated probes ($^{\circ}C$).

The probe length was longer than the sapwood thickness of some sampled trees. To avoid the underestimation of F_d , we used the corrected values (ΔT_C) rather than the measured values (ΔT) in these trees (Clearwater et al., 1999):

$$\Delta T_C = (\Delta T - (1 - a)\Delta T'_M) / a, \quad (3)$$

where ΔT_C and $\Delta T'_M$ are the actual temperature differences between heated and unheated probes in the conductive sapwood and in the inactive xylem ($^{\circ}C$), respectively; a is the length ratio of sap wood to probe; and $\Delta T'_M$ is equal to ΔT_M in Equation 2.

As F_d values are correlated with whole tree water consumption (Steppe et al., 2010), this value was used as an index to evaluate variations in transpiration. In addition, species specific calibration has been suggested (Du et al., 2011) and the underestimated value with thermal dissipation method should be considered when Granier-type probes data were used for whole tree water consumption calculation (Steppe et al., 2010). Therefore, the normalized F_d (SF_n) rather

than whole-tree water consumption was used for diurnal and daily variation analyses as suggested by Du et al. (2011). The SF_n was calculated by dividing all F_d values for each replicate tree by the maximum during the observation period. Each replicate tree had a maximum SF_n of 1, and the average normalized SF_n was calculated among replicates within species.

Table 1 Biometric variables of monitored species, including tree height, trunk diameter at breast or ground height, sapwood width, and canopy radius for *P. tabuliformis* and *H. rhamnoides* in both pure and mixed plantations

Plantation type	No.	Height (m)	Trunk diameter (mm)	Sapwood width (mm)	Canopy radius (m)
Pure plantation	1	3.49	42	15	1.50
	2	3.46	61	20	1.56
	3	3.00	54	18	1.35
	4	3.40	60	19	1.01
	5	3.74	52	16	1.28
	6	3.90	65	20	1.33
	7	3.77	50	17	1.21
	1	3.54	40	8	0.98
	2	3.00	48	8	0.84
	3	3.00	50	8	1.17
	4	3.84	63	10	0.93
	5	2.94	58	9	0.86
Mixed plantation	6	3.00	36	8	0.94
	1	3.90	70	22	1.20
	2	3.80	65	21	1.22
	3	3.44	54	17	1.18
	4	4.10	68	23	1.33
	5	4.56	65	18	1.48
	6	3.10	43	16	1.21
	1	4.20	67	8	1.05
	2	3.00	48	8	0.95
	3	3.20	53	7	1.11
	4	4.40	72	11	1.24
	5	2.60	38	8	0.89
	6	4.32	63	8	1.15

2.4 Investigation of root systems

In July 2015, 3 individual trees of *P. tabuliformis* and *H. rhamnoides* with approximately average trunk diameter and canopy radius (standard individual) were selected around each of 3 corresponding research plantations for whole plant root excavation. In pure plantation, the average canopy radius for standard individual of *P. tabuliformis* and *H. rhamnoides* was 1.38 (± 0.15) and 0.92 (± 0.09) m, respectively. In mixed plantation, the average canopy radius for standard individual of *P. tabuliformis* and *H. rhamnoides* was 1.19 (± 0.08) and 0.9 (± 0.11) m, respectively. Therefore, the corresponding radius of the majority of lateral roots was approximately 2.76 and 1.84 m for *P. tabuliformis* and *H. rhamnoides* in pure plantations, respectively; and was approximately 2.38 and 1.80 m for *P. tabuliformis* and *H. rhamnoides* in mixed plantation, respectively. The 3-m radius and 2-m depth for root excavations captured the majority of lateral and vertical roots for each selected standard individual. A spade was used to dig up the roots at 10 cm depth intervals, starting from the plant trunk to the edge of the plant canopy. Then, the fine roots (diameter < 2 mm) were manually selected, and their surface area was

calculated for each 10 cm of the depth profile using WinRHIZO (Regent Instruments Inc., Quebec, Canada).

2.5 Leaf water potential, stomatal conductance, and photosynthetic rate measurements

We examined leaf water potential, g_s , and P_r in 16 of 25 *SF* monitored individuals (4 individuals per species in each plantation) at midday (11:00–14:00, LST) three times per month from June to September, 2015 (Table 1). Three well-expanded leaves were selected from each monitored individual. A LI-6400 analyzer (Li-Cor Inc., USA) was used to measure g_s and P_r under approximately natural conditions (Du et al., 2011). In addition, predawn leaf water potential (Ψ_{pd} , 05:00–06:00) and midday leaf water potential (Ψ_m , 11:00–14:00) were measured on nearby leaves on the same individual used for g_s and P_r measurements with a PMS-1515D analyzer (PMS Instrument, Corvallis, OR, USA).

2.6 Threshold-delay model

The threshold-delay model suggests that there are upper and lower precipitation thresholds which stimulate plant water consumption (Ogle and Reynolds, 2004). This model incorporates the duration of rainfall pulse and the speed of plant response (Zeppel et al., 2008):

$$y_t = ky_{t-1} + \delta_t, \quad (4)$$

$$y_t = \min \left[y_{\max} (1-k), \delta_t^* (1-y_{t-1}/y_{\max}) \right], \quad (5)$$

$$\delta_t^* = \begin{cases} (\delta_{\max} / (R^U - R^L)) (R_{t-\tau} - R^L) & R^L < R_{t-\tau} < R^U \\ 0 & R_{t-\tau} \leq R^L \\ \delta_{\max} & R_{t-\tau} \geq R^U \end{cases}, \quad (6)$$

where y_t is the SF_n in this study; y_{t-1} is the antecedent SF_n ; y_{\max} is the maximum response SF_n ; δ_t , δ_t^* , and δ_{\max} are the potential, actual, and maximum potential response parameters, respectively; R^U and R^L are the upper and lower rainfall thresholds (mm), respectively; $R_{t-\tau}$ is the effective rainfall amount (mm); τ is the time lag when the significant increases in SF_n were observed after $R_{t-\tau}$ (d); k is the reduction rate (d); and t is the response time (d).

After testing for normal distribution and homogeneity of variance, we identified the rainfall threshold through one-way analysis of variance (ANOVA) and Tukey's HSD test. Then, the threshold-delay model was calculated by multiple linear regression (Ogle and Reynolds, 2004).

2.7 Statistical analysis

Relative response in daily SF_n was calculated as $(X_{\max} - X_{\text{before}}) / X_{\text{before}} \times 100\%$, where, X_{before} and X_{\max} represent the SF_n from the first day before a rainfall and the maximum SF_n after rainfall, respectively. Significant relative changes in SF_n for *P. tabuliformis* in pure and mixed plantations, and *H. rhamnoides* in pure and mixed plantations in response to rainfall were identified through ANOVA and Tukey's HSD test, after testing for a normal distribution and homogeneity of variance. Rainfall classes of 0–5, 5–10 and >15 mm were used for significant test, but a rainfall class of 10–15 mm was not used because only 11 mm rainfall (DOY 222–226) was observed during the study period.

Significant differences in SF_n , leaf water potential, g_s , and P_r between species in pure and mixed plantations were identified by independent samples *t*-test, after testing for the normality and homogeneity of variances. Moreover, we also evaluated the effects of mixed afforestation on SF_n , leaf water potential, g_s , and P_r through independent samples *t*-test based on significant difference analyses of these variables for specific species in pure and mixed plantations.

In addition, the relationship between Ψ_{pd} and corresponding maximum SF_n has been used to assess the effect of stomatal control on hydraulic characteristics (Thomas et al., 2008). The significant difference in the slope of a SF_n and Ψ_{pd} linear regression can be tested through a General Linear Model (GLM) (Wei et al., 2013). SPSS 18.0 was used for all the statistical and regression analyses (SPSS Inc., Chicago, IL, USA), and the significant level was set at $P < 0.05$ level.

3 Results

3.1 Variation of environmental variables

There was 120.8 mm of rainfall during the observation period (DOY 156–269), which was the lowest value since 1988 and accounted for 33.8% of the mean annual precipitation amount between 1988 and 2014 in the corresponding period. Although rainfall gradually increased during the later observation period (Fig. 1a), the daily average rainfall ($1.1 (\pm 2.4)$ mm/d) represented only 8.4% of the corresponding ET_p . This lack of sufficient rainfall and high water demand may have resulted in drought stress for these studied plantations, according to the monthly variation of Budyko's aridity index (Table 2).

The SWC at 10 cm depth showed the largest fluctuation with rainfall (Fig. 1; Table 3), and the SWCs at depth 100 and 150 cm gradually decreased during the observation period for the three plantations, which suggested that rainfall had less effect on SWC in deep soil. The highest daily averaged SWCs were observed at depth 50 cm for pure *P. tabuliformis* plantation, 100 cm for pure *H. rhamnoides* plantation, and 150 cm for mixed plantation. The lowest daily averaged SWCs also experienced the smallest coefficient of variation (CV) for each plantation, and could be observed at 150 cm depth for pure *P. tabuliformis* plantation, 20 cm depth for pure *H. rhamnoides* plantation, and 50 cm depth for mixed plantation (Table 3).

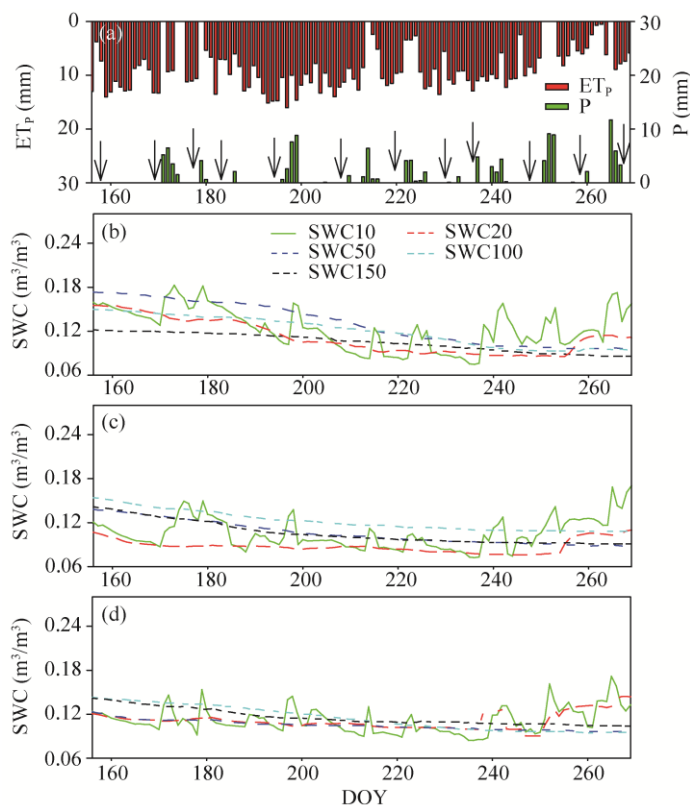


Fig. 1 Daily variation of environmental variables from DOY (day of the year) 156 to 269 (5 June–26 September). (a) rainfall amount (P) and potential evapotranspiration (ET_p); soil water content (SWC) at depths of 10, 20, 50, 100, and 150 cm (SWC10, SWC20, SWC50, SWC100, and SWC150) in (b) pure *P. tabuliformis* plantation, (c) pure *H. rhamnoides* plantation, and (d) mixed plantation. Vertical arrows in Figure 1a indicate leaf water potential, g_s (stomatal conductance), and P_r (photosynthetic rate) observation dates.

3.2 Daily and diurnal variations in SF_n and responses to rainfall

The daily SF_n for *P. tabuliformis* and *H. rhamnoides* in pure plantations generally exhibited a decreasing trend during the observation period; meanwhile, the daily SF_n for both these two species in mixed plantation exhibited a "U" type, with the higher value occurring in June and September (Fig. 2). The variation of daily SF_n for *P. tabuliformis* in the plantation was

Table 2 Monthly Budyko's aridity index in 2015 and average value between 2012 and 2014

Month	2015	2012–2014
January	0.05	0.03±0.03
February	0.21	0.37±0.29
March	0.15	0.21±0.10
April	0.16	0.59±0.34
May	0.11	0.45±0.07
June	0.08	0.95±0.06
July	0.04	3.16±1.97
August	0.13	1.46±0.24
September	0.29	2.01±0.59
October	0.23	0.24±0.13
November	0.37	0.40±0.02
December	0.11	0.09±0.01

Note: Budyko's aridity index is the ratio of the rainfall amount (P) to potential evapotranspiration (ET_p). An index smaller than 1.00 means the ecosystem has suffered drought stress. Mean±SD.

Table 3 Daily average and coefficient of variation (CV) of soil water content (SWC) at depths of 10, 20, 50, 100, and 150 cm (SWC10, SWC20, SWC50, SWC100, and SWC150) in three studied plots

		<i>P. tabuliformis</i> in pure plantation	<i>H. rhamnoides</i> in pure plantation	Mixed plantation
SWC10	Average (m^3/m^3)	0.12±0.03	0.11±0.02	0.11±0.02
	CV (%)	22.62	20.21	15.71
SWC20	Average (m^3/m^3)	0.11±0.02	0.09±0.01	0.11±0.01
	CV (%)	20.25	9.97	10.15
SWC50	Average (m^3/m^3)	0.13±0.03	0.11±0.02	0.10±0.01
	CV (%)	21.81	14.67	6.17
SWC100	Average (m^3/m^3)	0.12±0.02	0.12±0.01	0.11±0.02
	CV (%)	16.51	11.10	14.39
SWC150	Average (m^3/m^3)	0.10±0.01	0.11±0.02	0.12±0.01
	CV (%)	11.37	14.41	9.52

Note: CV is the ratio of standard deviation to mean value×100%. Mean±SD.

significantly different ($t=4.95$, $P<0.01$, $df=226$) from that for the same species in mixed plantation. However, there was no significant difference ($t=1.95$, $P=0.053$, $df=226$) in daily variation of SF_n for *H. rhamnoides* in pure and mixed plantations. Generally, the relative response of SF_n for these two species significantly increased ($P<0.05$, $df=2$) among three rainfall classes in both pure and mixed plantations (Fig. 3), when 10–15 mm class was not considered. However, no significant difference was observed either between rainfall classes of 5–10 and >15 mm for *P. tabuliformis* in pure plantation ($P=0.09$, $df=7$), or between rainfall classes of 0–5 and 5–10 mm for *H. rhamnoides* in pure plantation ($P=0.14$, $df=7$). Moreover, the CVs of SF_n for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 39.1% and 37.59%, and were 43.64% and 36.58% for corresponding species in mixed plantation, respectively (Table 4).

Figures 4 showed the diurnal variation of SF_n . The values of SF_n for *P. tabuliformis* and *H. rhamnoides* in pure plantations increased from a minimum at midnight to a maximum at noon time, and exhibited a unimodal curve (Figs. 4a and c). In pure plantation, the half hourly average SF_n values for *P. tabuliformis* and *H. rhamnoides* after rainfall increased from 0.27 (±0.26) to 0.32 (±0.30) and from 0.24 (±0.23) to 0.35 (±0.33), respectively. The SF_n for *P. tabuliformis* in mixed plantation followed a similar diurnal variation as that of *P. tabuliformis* in pure plantation. However, *H. rhamnoides* in mixed plantation showed a bimodal curve before rainfall and a unimodal curve after rainfall (Fig. 4d). Furthermore, the half hourly average SF_n values for *P. tabuliformis* and *H. rhamnoides* in mixed plantation after rainfall increased from 0.23 (±0.24) to

0.3 (± 0.31) and from 0.21 (± 0.19) to 0.32 (± 0.30), respectively.

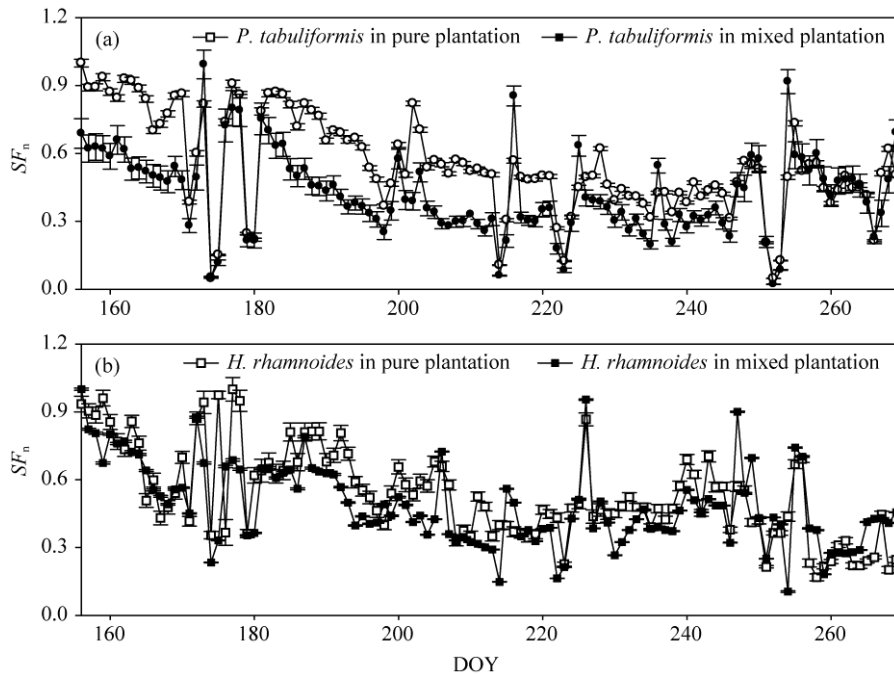


Fig. 2 Variation of daily normalized sap flow (SF_n). (a) *P. tabuliformis* and (b) *H. rhamnoides* in both pure and mixed plantations during DOY 156–269 (5 June to 26 September). Error bars indicate the standard deviation.

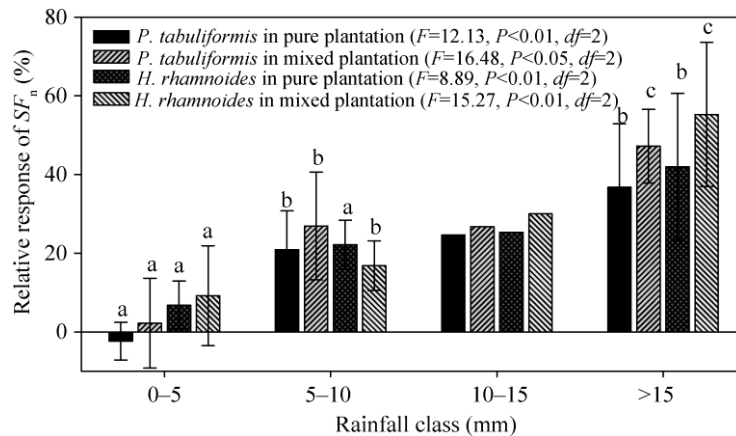


Fig. 3 Relative response of SF_n to rainfall class. Error bars indicate the standard deviation. Lowercase letters indicate a significant difference in daily SF_n responses among rainfall classes in the specific species in pure or mixed plantation. The ANOVA test parameters for relative response of SF_n among three rainfall classes (0–5, 5–10 and >15 mm) are also presented. The rainfall class of 10–15 mm was not used for the significant test.

The lower thresholds of rainfall for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 9.6 and 11.0 mm, and the values for corresponding species in mixed plantation were 6.5 and 8.8 mm, respectively, based on the threshold-delay model (Table 5). The upper-thresholds of rainfall for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 16.7 and 20.9 mm, and the values for corresponding species in mixed plantation were 19.6 and 22.1 mm, respectively. The lag times after an effective rainfall event were 1.15 and 1.76 d for *P. tabuliformis* and *H. rhamnoides* in pure plantation, and 0.86 and 1.61 d for corresponding species in mixed plantation, respectively.

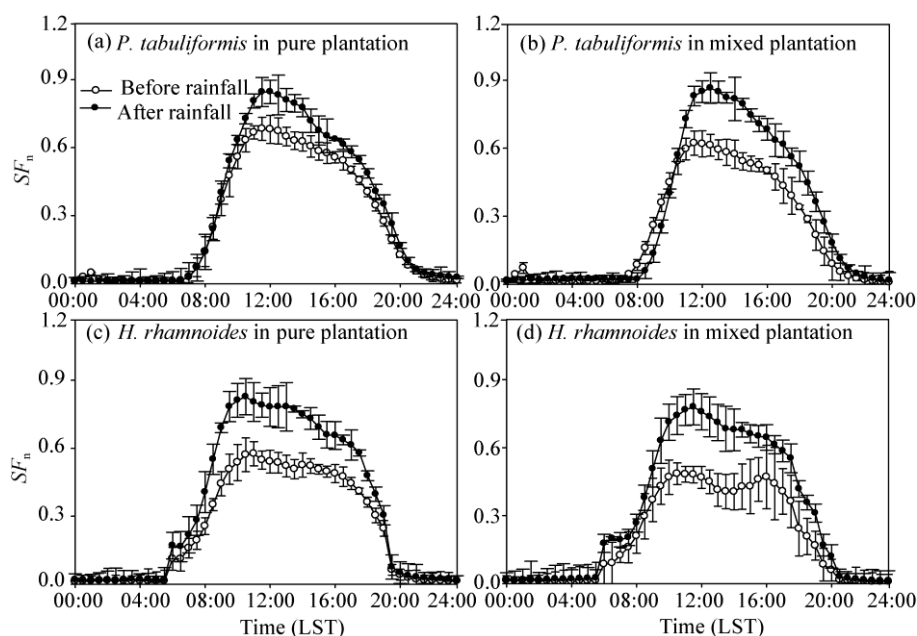
3.3 Variation of leaf water potential and relationship between Ψ_{pd} and maximum SF_n

In pure and mixed plantations, Ψ_{pd} and Ψ_m for *P. tabuliformis* and *H. rhamnoides* generally

Table 4 Daily average and CV of normalized sap flow (SF_n), predawn and midday leaf water potential (Ψ_{pd} and Ψ_m , respectively), stomatal conductance (g_s), and photosynthetic rate (P_r) for *P. tabuliformis* and *H. rhamnoides* in both pure and mixed plantations

		<i>P. tabuliformis</i> in pure plantation	<i>P. tabuliformis</i> in mixed plantation	<i>H. rhamnoides</i> in pure plantation	<i>H. rhamnoides</i> in mixed plantation
SF_n	Average	0.55±0.22	0.42±0.18	0.54±0.20	0.49±0.18
	CV (%)	39.10	43.64	37.59	36.58
Ψ_{pd}	Average (Mpa)	-1.08±0.29	-1.03±0.36	-1.03±0.20	-1.33±0.41
	CV (%)	26.32	35.13	19.91	31.12
Ψ_m	Average (Mpa)	-1.65±0.32	-1.55±0.34	-1.96±0.37	-2.45±0.47
	CV (%)	19.18	21.85	18.97	18.99
g_s	Average (mol/(m ² ·s))	0.11±0.04	0.07±0.04	0.15±0.04	0.12±0.04
	CV (%)	34.53	53.03	28.02	31.22
P_r	Average (μmol CO ₂ /(m ² ·s))	4.58±1.56	2.65±1.55	5.90±1.41	4.99±1.55
	CV (%)	34.13	58.48	23.93	31.08

Note: CV is the ratio of standard deviation to mean value×100%. Mean±SD.

**Fig. 4** Diurnal variation of SF_n in response to rainfall pulse. (a) *P. tabuliformis* in pure plantation, (b) *P. tabuliformis* in mixed plantation, (c) *H. rhamnoides* in pure plantation, and (d) *H. rhamnoides* in mixed plantation during DOY 156–269 (5 June–26 September). Before and after rainfall indicated the SF_n before a rainfall event and the maximum value occurred after the rain events. The day after rainfall was chosen according to the method in threshold-delay model. Error bars indicate the standard deviation.**Table 5** Threshold-delay model parameters for *P. tabuliformis* and *H. rhamnoides* in both pure and mixed plantations during the observation period

	R^L (mm)	R^U (mm)	k (d)	τ (d)
Pure <i>P. tabuliformis</i>	9.6	17.5	0.13	1.15
Pure <i>H. rhamnoides</i>	11.0	16.7	0.04	1.76
Mixed <i>P. tabuliformis</i>	6.5	22.1	0.21	0.86
Mixed <i>H. rhamnoides</i>	8.9	18.9	0.06	1.61

Note: R^L and R^U are the lower and upper thresholds of rainfall, respectively; k is the reduction rate; and τ is the time lag.

experienced a "U" type, with the higher values occurring in June and September (Fig. 5). In addition, the increased Ψ_m was also observed for *H. rhamnoides* in pure and mixed plantations

during DOY 171–174. Both in pure ($t=0.55$, $P=0.59$, $df=22$) and mixed ($t=1.88$, $P=0.74$, $df=22$) plantations, Ψ_{pd} did not significantly differ between *P. tabuliformis* and *H. rhamnoides*. Moreover, in both pure ($t=2.2$, $P<0.05$, $df=22$) and mixed ($t=5.41$, $P<0.001$, $df=22$) plantations, Ψ_m in the former species was significantly higher than in the latter species.

Mixed afforestation did not significantly affect the Ψ_{pd} ($t=0.40$, $P=0.7$, $df=22$) or Ψ_m ($t=0.74$, $P=0.47$, $df=22$) for *P. tabuliformis*; however, it significantly decreased Ψ_{pd} ($t=2.26$, $P<0.05$, $df=22$) and Ψ_m ($t=2.85$, $P<0.01$, $df=22$) for *H. rhamnoides*. Furthermore, mixed afforestation enhanced the CVs of Ψ_{pd} for *P. tabuliformis* and *H. rhamnoides*, but had less effect on the CVs of Ψ_m for these species (Table 4).

In pure and mixed plantations, there were no significant relationships between Ψ_{pd} and maximum SF_n for *H. rhamnoides*; however, maximum SF_n gradually dropped with decreasing Ψ_{pd} for *P. tabuliformis* in these plantations (Table 6). In addition, mixed afforestation significantly offset the sensitivity of maximum SF_n to Ψ_{pd} for *P. tabuliformis* ($F=5.78$, $P<0.05$, $df=1$), which suggested that this species in mixed plantation experienced stronger stomatal control on water consumption than in pure plantation.

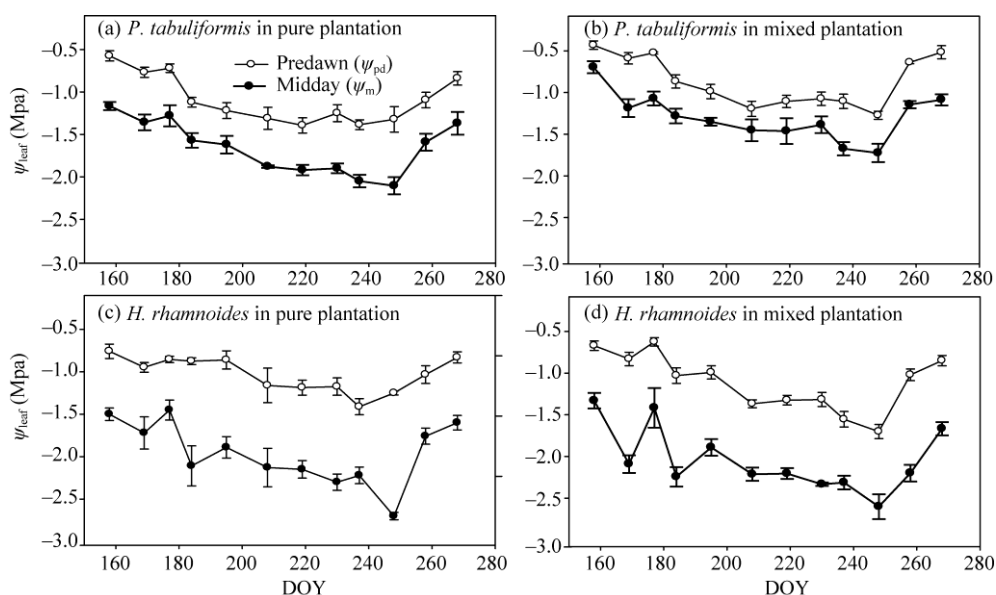


Fig. 5 Variation of predawn (Ψ_{pd}) and midday leaf water potential (Ψ_m), respectively. (a) *P. tabuliformis* in pure plantation, (b) *P. tabuliformis* in mixed plantation, (c) *H. rhamnoides* in pure plantation, and (d) *H. rhamnoides* in mixed plantation during DOY 156–269 (5 June–26 September). Error bars indicate the standard deviation.

Table 6 Maximum SF_n as a function of predawn leaf water potential (Ψ_{pd}) for *P. tabuliformis* and *H. rhamnoides* in pure and mixed plantations

Species	Equation	R^2	P	n
<i>P. tabuliformis</i> in pure plantation	$y=0.55x+1.25$	0.80	<0.001	12
<i>H. rhamnoides</i> in pure plantation	$y=0.43x+0.94$	0.30	0.070	12
<i>P. tabuliformis</i> in mixed plantation	$y=0.23x+0.84$	0.37	<0.050	12
<i>H. rhamnoides</i> in mixed plantation	$y=0.23x+0.80$	0.28	0.080	12

3.4 Variation of g_s and P_r

In pure and mixed plantations, g_s and P_r for *P. tabuliformis* and *H. rhamnoides* exhibited similar variation to that of leaf water potential, with the higher values occurring in June and September (Fig. 6). The increased g_s was observed for *H. rhamnoides* in pure and mixed plantations during DOY 171–174. In addition, the increased P_r was observed for *P. tabuliformis* in pure and mixed plantations and for *H. rhamnoides* in pure plantation during DOY 171–174. In pure plantation, both g_s and P_r for *H. rhamnoides* were significantly higher ($t=2.15$, $P<0.05$, $df=22$ and $t=2.17$, $P<0.05$, $df=22$, respectively) than the corresponding values for *P. tabuliformis*. In mixed

plantation, both g_s and P_r for *H. rhamnoides* were also significantly higher ($t=3.47$, $P<0.05$, $df=22$ and $t=3.7$, $P<0.01$, $df=22$, respectively) than the corresponding values for *P. tabuliformis* (Fig. 6).

Moreover, mixed afforestation significantly decreased both g_s ($t=2.96$, $P<0.01$, $df=22$) and P_r ($t=3.04$, $P<0.01$, $df=22$) for *P. tabuliformis*, but had no significant effect on g_s ($t=1.72$, $P=0.10$, $df=22$) and P_r ($t=1.51$, $P=0.15$, $df=22$) for *H. rhamnoides*. In addition, mixed afforestation enhanced the CVs of g_s and P_r for *P. tabuliformis*, but had less effect on the corresponding values for *H. rhamnoides* (Table 4).

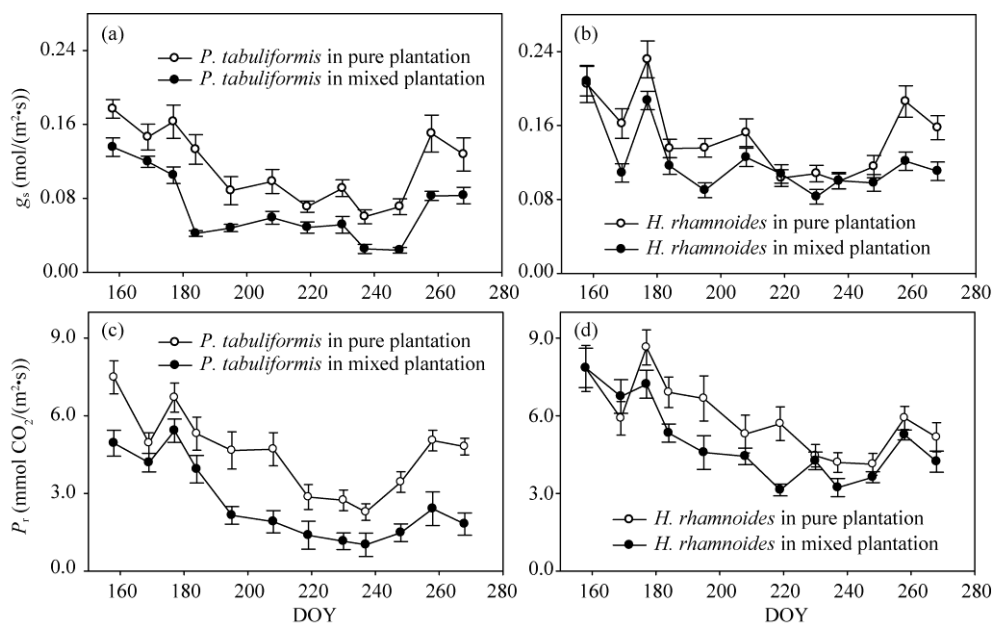


Fig. 6 Variations of stomatal conductance (g_s) and photosynthetic rate (P_r). *P. tabuliformis* in (a) pure and (c) mixed plantations, *H. rhamnoides* in (b) pure and (d) mixed plantations during DOY 156–269 (5 June–26 September). Error bars indicate the standard deviation.

4 Discussion

4.1 Sap flow characteristics and its response to rainfall in pure plantations

Similar to other studies in semi-arid regions (Swaffer et al., 2014; Jian et al., 2016), departure in SF_n in response to rainfall pulse for *P. tabuliformis* and *H. rhamnoides* indicated that sap flow in response to rainfall pulse underlying drought was species dependent. Previous studies indicated that coniferous species usually exhibited a strong self-regulation to maintain water consumption under drought conditions and were more sensitive to rainfall than broad-leaved species (Teklemariam et al., 2010; Zha et al., 2010; Wen et al., 2017). Moreover, the response of SF_n to rainfall pulse also depends on both rainfall characteristics (Burgess, 2006) and other environmental conditions, such as drought extent (Reyes-Acosta and Lubczynski, 2014). Large rainfall events may relieve drought conditions and small rainfall amounts may only wet the plant surface (Reynolds et al., 2004). Previous studies in shrubs (Jian et al., 2015) and trees (Du et al., 2011) reported that 5.0 mm was the threshold rainfall amount to effectively influence water consumption in the Loess Plateau. However, 9.6 and 11.0 mm were required as the lowest rainfall amounts to significantly increase SF_n for *P. tabuliformis* and *H. rhamnoides* in pure plantations, respectively, which may be attributed to severe drought stress because the rainfall in 2015 was the lowest since 1988 (Fig. 2). Zhao and Liu (2010) and Jian et al. (2016) also suggested that 13.0 mm was the upper-threshold of rainfall to affect plant water consumption in the Chinese Loess Plateau. However, 16.7 and 20.9 mm were required as the upper rainfall amounts for *P. tabuliformis* and *H. rhamnoides*, respectively, and may also attribute to the severe drought stress.

Moreover, Zencich et al. (2002) and Tang et al. (2014) suggested that diverse root vertical distribution explained the different species responses to rainfall events. For example,

shallow-rooted *Hibbertia hypericoides* responded rapidly to rainfall pulses; however, deep-rooted *Banksia ilicifolia* did not respond to rainfall even if it reached 10.0 mm (Zencich et al., 2002). In the studied pure plantations, more fine roots distributed in the upper soil layer of *P. tabuliformis* could partially explain shorter time response ($\tau=1.15$) to rainfall compared with *H. rhamnoides* ($\tau=1.76$; Fig. 7). The higher R^U , smaller R^L , and τ for *P. tabuliformis* indicated that this species experienced high water demand and was more sensitive to rainfall pulses than the species *H. rhamnoides*. These results were consistent with studies in the hilly region of the Chinese Loess Plateau by Wen et al. (2017), which suggested that *P. tabuliformis* was more sensitive to rainfall than *H. rhamnoides*, by comparing the relative response of diurnal variation in transpiration before and after rainfall. Furthermore, the anatomical structure of xylem needs further analysis to well understand the water demand and rainfall pulse responses of each species (Xu and Li, 2006).

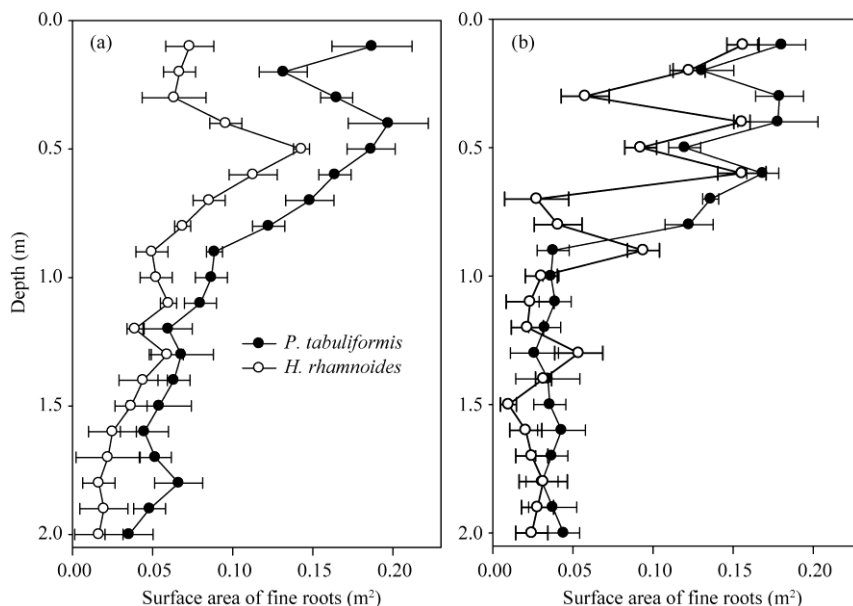


Fig. 7 Vertical distribution of surface area of fine root (diameter < 2 mm). *P. tabuliformis* and *H. rhamnoides* in (a) pure and (b) mixed plantations. Error bars indicate the standard deviation.

4.2 Trade-off between stomatal control, leaf water potential, and photosynthesis in pure plantations

Previous studies suggested that the contrasting hydraulic traits among species under identical weather conditions probably resulted from both water uptake capacity (Xu and Li, 2006) and their optimized trade-off between carbon gain and water loss through photosynthesis (Sperry and Hacke, 2002). Ψ_{pd} can be substituted for soil water potential in contact with the roots (Bucci et al., 2004). Although there was no significant difference between Ψ_{pd} for these two species, significantly ($P < 0.05$) higher Ψ_m was observed for *P. tabuliformis* than for *H. rhamnoides*. The results indicated that the former species maintained stable water status to avoid embolism damage and for protection of the water conducting system.

In the studied pure plantations, the observed decrease in maximum SF_n with decreasing Ψ_{pd} for *P. tabuliformis* was consistent with the hypothesis of Meinzer et al. (1999), who stated that high hydraulic constraints and water demand can lead to strong stomatal limitations to photosynthesis and transpiration. In contrast, no significant relationship between maximum SF_n and Ψ_{pd} was observed for *H. rhamnoides* indicating that there was a weak stomatal limitation on transpiration and photosynthesis for this species. Xu et al. (2011) suggested that high concentrations of osmotically active substances in *H. rhamnoides* allowed wide osmotic adjustment and maintenance of stable leaf cell turgor pressure, and thus allowed stomatal opening and maintenance of photosynthesis. Moreover, similar to *P. deulis* (West et al., 2007) and *Virola michelii* (Bonal and Guehl, 2001), *P. tabuliformis* can be considered as an isohydric species and can thus adequately maintain Ψ_m through strong stomatal limitation, with the low g_s and P_r during

drought. However, *H. rhamnoides* can be considered as an anisohydric species, maintaining g_s and P_r at low Ψ_m expense. Similar physiological adjustments were observed in *Juniperus osteosperma* (West et al., 2007) and *E. grandis* (Zhu et al., 2015).

4.3 Mixed afforestation effects on *P. tabuliformis* and *H. rhamnoides*

Facilitative interactions in relation to water resources can lead to stable co-existence, however, competition for water resources may induce exclusion of species (Xu and Li, 2006). Co-existing species in natural forest usually exhibit different physiological or morphological adjustments to minimize competition for water during prolonged drought periods (Trubat et al., 2006; Yang et al., 2015). This facilitative interaction has also been observed among species in plantations even in seasonal drought or semi-arid water limited regions (Wu et al., 2017; Zhang et al., 2017). For example, Zhang et al. (2017) suggested the dense canopy cover of *P. tabuliformis* can reduce the evaporation of soil water in surface layers, which may benefit co-existing species, such as *Platycladus orientalis*, in the dryland Loess Plateau of China. However, in the semi-arid Loess Plateau of China in the present study, although contrasting physiological adjustments of *P. tabuliformis* and *H. rhamnoides* were observed in mixed plantations (Figs. 5 and 6), mixed afforestation significantly altered SF_n characteristics and rainfall pulse sensitivity in *P. tabuliformis*. Mixed afforestation reduced 32.3% and 25.2% of R^L and τ for *P. tabuliformis*, respectively. However, the effect of mixed plantation only reduced the corresponding values of R^L and τ to 19.1% and 8.5% for *H. rhamnoides* (Table 5). In addition, mixed plantation increased 26.3% and 13.2% of R^U for *P. tabuliformis* and *H. rhamnoides*, respectively. Previous studies also indicated that, compared with isohydric species, anisohydric species such as *Acer saccharum* and *E. gomphocephala* may be more suitable to drought-prone habitats (Franks et al., 2007; West et al., 2007). However, under prolonged drought and less precipitation water input, anisohydric species may experience xylem embolism even mortality (Xu and Li, 2006), and isohydric species may suffer from carbon starvation (McDowell et al., 2008). The threshold value of leaf water potential causing 100% stem cavitation for *P. tabuliformis* and carbon gain to avoid carbon starvation for *H. rhamnoides* needs further investigation to assess the drought adaptive capacity of these two species.

Competition among co-occurring species may be apparent through root morphology characteristics such as architecture of fine root systems (Sperry and Hacke, 2002; Xu et al., 2007). Although accurate water source was not analyzed using stable isotopes in the present study, the overlap in root distribution of co-occurring species may result in water competition (Schwinning and Ehleringer, 2001). In response to prolonged drought in desert regions, *H. rhamnoides* also exhibited root morphology plasticity (Xu et al., 2007). In the studied mixed plantation, *H. rhamnoides* developed more shallow roots and a similar root distribution to *P. tabuliformis* especially in the upper 40 cm of soil (Fig. 7). West et al. (2007) suggested that shallow roots may maximize extraction of water before it is lost to evaporation and maximize the uptake of nutrients, as nutrient concentrations are highest near the soil surface. Indeed, the total nitrogen (0.53%) and phosphorus (0.04%) contents at 0–40 cm soil depth were 2.20 and 1.97 times more than that at 40–100 cm soil depth. Thus, *H. rhamnoides* and *P. tabuliformis* in mixed plantation may have competed for limited water and nutrient reserves. Therefore, competition for both water and nutrients should be further investigated to adequately evaluate mixed afforestation of these species.

5 Conclusions

This study demonstrated that *H. rhamnoides* and *P. tabuliformis* adopted contrasting strategies to cope with drought in 2015. Compared with *H. rhamnoides*, *P. tabuliformis* was more sensitive to rainfall pulse in pure plantation. *P. tabuliformis* displayed isohydric behavior through strong stomatal limitation, and *H. rhamnoides* displayed anisohydric behavior. Mixed afforestation enhanced more rainfall pulse sensitivity and water demand for *P. tabuliformis*. However, mixed afforestation did not significantly affect the rainfall pulse sensitivity of *H. rhamnoides* at the expense of decreased leaf water potential status. Therefore, the mixed afforestation of these two species should be further considered for "Grain-for-Green" projects in this region.

Acknowledgments

This research was supported by the National Key R&D Program of China (2017YFA0604801), the National Natural Science Foundation of China (41501576), the China Special Fund for Meteorological Research in the Public Interest (Major Projects) (GYHY201506001-3), and the Fundamental Research Funds for the Central Universities (2452016105).

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Supplementary figure

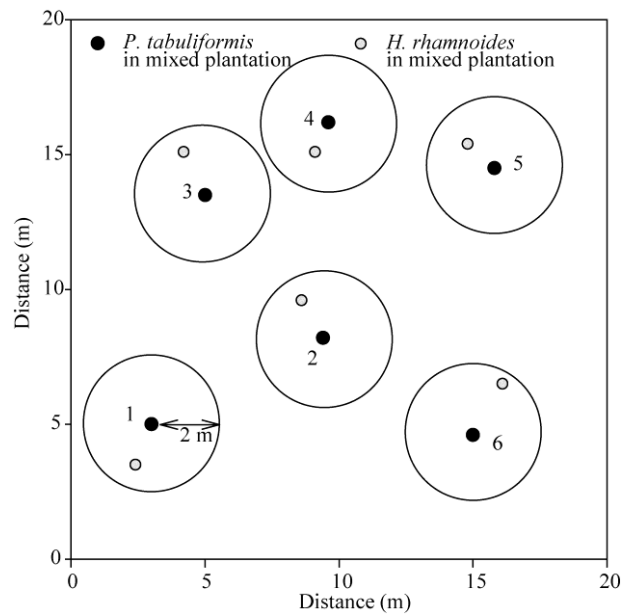


Fig. S1 Schematic of the local neighborhood for 6 pairs of selected *P. tabuliformis* and *H. rhamnoides* individuals in mixed plantation. A distance of 2 m was measured from center of the trunk to the edge of canopy for each *P. tabuliformis* individual, and the number (1–6) around *P. tabuliformis* individual was the same tree individual number in Table 1 in mixed plantation.